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38

**The Food, Growth and Population
Structure of Salmon and Trout in two
Streams in the Scottish Highlands**

By HENRY J. EGGLISHAW, B.Sc., Ph.D.

Freshwater Fisheries Laboratory, Pitlochry

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The Food, Growth and Population Structure
of Salmon and Trout in two Streams
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The Food, Growth and Population Structure of Salmon and Trout in two Streams in the Scottish Highlands

INTRODUCTION

The food available to a species is usually considered a prime factor in its productivity. This is particularly so in the case of animals such as salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) which can vary greatly in their rate of growth, which continue growing after reaching maturity and can continue to do so throughout their lives. In Great Britain, salmon and trout, fish of commercial and recreative value, have attracted several workers to the study of their food and related subjects, and there is now a considerable amount of knowledge from waters in different parts of the country (e.g. for salmon Allen (1940, 1941a) and Carpenter (1940) on rivers in northern England, Allen (1941a, 1941b) on Thurso River in northern Scotland; for trout Horton (1961) on a stream in southern England, Neill (1938) on the River Don, Scotland and for both species Thomas (1962) on the River Teify, Wales). The present paper deals with the feeding biology of young salmon and trout in two streams of different character in the Central Highlands of Scotland, an area in which little work has previously been carried out. It includes problems, particularly those concerning the variation in food present in fish stomachs, the distribution of the benthic fauna and the heterogeneity of the stream environment, not considered by other workers. In addition, in view of the large amount of stocking of streams and rivers with salmon that is carried out by various bodies, the opportunity was taken to investigate the feeding of hatchery reared salmon that had been introduced to a stream.

THE STREAMS STUDIED

The main observations were made on the Shelligan Burn, a tributary of the River Almond, and on the headwaters of the River Almond. Both streams are in Perthshire.

The Shelligan Burn, rising at an altitude of about 550 m, flows south-eastwards for 3.2 km and then east for a further 2.4 km to join the River Almond. The 400 m length of stream studied is 4 km from its source and near to where the stream is crossed by a road (Nat. Grid ref. 37/941291). Here the Shelligan Burn is at an altitude of 183 m and flows through agricultural land and sheep and cattle pasture. There are deciduous trees, chiefly oak and beech, on the west bank of the stream and along the margins of neighbouring fields. Upstream from the site studied there is a conifer plantation on the west bank and beyond this the surroundings are heather moorland. The width of the stream at the site studied is very even throughout its length and is 4 m. Before reaching the site the Shelligan Burn flows over sandstone and quartzite.

The headwaters of the River Almond (subsequently referred to as the River Almond) rise at about 820 m and flow eastwards. The site studied (Nat. Grid ref. 27/798334) lies about 10 km from the source and 18 km upstream from where it is joined by the Shelligan Burn. The site, 200 m in length, is at an altitude of 290 m and is surrounded by heather moor and rough sheep-grazing land. There are no trees at the site. Approximately 200 m from the river bank and 500 m upstream from the site there is a plantation of mixed larch and spruce trees, 10–12 years old. The surroundings are noticeably much poorer as regards vegetation than the surroundings of the Shelligan Burn examined. The stream, 16 m wide, is four times wider than the Shelligan Burn. Upstream of the site studied the River Almond flows over quartzite and mica schist. The straight-line distance between the site on the Shelligan Burn and that on the River Almond is 16 km.

The substrate of the site of the Shelligan Burn consists of stones, mostly less than 30 cm in diameter, lying on stones embedded in gravel and sand. The site is chiefly riffle with a depth under normal water conditions of between 10 cm and 18 cm mainly, but up to 25 cm in places, and there are some pools which reach 60 cm depth. Among the stones and gravel there is a large amount of disintegrating fragments of leaves, stems and seed cases (p. 6). There are submerged mosses attached to stones in the faster flowing parts of the riffle stretches.

The substrate of the site on the River Almond is similar with regard to stone size to that of the site on the Shelligan Burn. The site again is chiefly riffle with a depth of 10–18 cm and there are some pools up to 60 cm

deep. Compared with the Shelligan Burn there is less allochthonic plant material (p. 7), reflecting the paucity of the surroundings. There are no submerged mosses in the River Almond headwaters.

The Shelligan Burn is chemically richer than the headwaters of the River Almond (Table 1).

Both the Shelligan Burn and the River Almond headwaters are spawning streams for salmon and trout (including sea trout), and eels (*Anguilla anguilla* (L.)) are present in the Shelligan Burn.

THE BOTTOM FAUNA

Quantitative samples of bottom fauna were taken each month from both streams from March 1962 until April 1963, except in January and February 1963 when the River Almond headwaters were inaccessible due to snow. The samples were taken for three purposes; to investigate factors affecting the distribution of the bottom fauna (Egglishaw, 1964), to compare the standing stock present in the streams throughout the year and to discover the relationship between the bottom fauna and the nature and amount of food eaten by the salmon and trout. All of the samples were taken within 50 m lengths of riffles that were within the fish sampling areas of both streams. The technique used depends on allowing the water current to wash animals from an area of substrate, disturbed by the investigator, into a hand net held on the downstream side of the sampling site. The hand-net used is pyramid-shaped, made of grit-gauze, 12 meshes per cm, attached to a square frame with 24 cm sides. Each sample was taken in a depth of water up to about 20 cm and at a site where the stones were 8–25 cm in diameter. The current speed over all sites was the same as far as could be observed. Ten samples were taken each month. It is thought that the collections are representative of the freely moving animals in the riffle, but animals which cling to the substrate (e.g. *Simulium* spp., Hydropsychidae) may not have been collected so effectively.

A full account of the bottom fauna is to be published elsewhere (Egglishaw and Mackay, in press). Here it is necessary to mention only some aspects that directly concern the feeding habits of the fish populations.

The names of the most abundant organisms present in the streams in spring (April and May) and summer (June) are given in Table 2. These months are chosen so as to include all the commonest species found during the year. The bottom fauna collected in these months was separated into 51 taxonomic categories. All categories that comprised 4 % or more of the fauna of either stream are included in the table. Between six and eight of the categories make up about three-quarters of the bottom fauna collected from each stream at each time. In addition to the organisms listed in the table, in spring the Plecoptera *Leuctra hippopus* (Kempny), *Chloroperla tripunctata* (Scopoli), *Isoperla grammatica* (Poda), *Protonemura meyeri* (Pictet), *Perla bipunctata* (Pictet), *Dinocras cephalotes* (Curtis), *Brachyptera risi* (Morton); Trichoptera of five families; the Coleoptera *Limnius tuberculatus* Müller, *Latelmis volkmari* (Panzer) and *Helmis maugei* Bedel; larvae of *Dicranota* spp., *Simulium* spp., Clinocerinae, Ceratopogonidae; *Crenobia alpina* (Dana), Hydracarina and *Gammarus pulex* (L) were all present in both streams. *Leuctra moselyi* Morton was present in both streams in June. The only species restricted to one of the streams were *Wormaldia* spp. to the River Almond and Limnephilidae, *Hydraena gracilis* Germar, *Oreodytes rivalis* (Gyllenhal) and *Ancylastrum fluviatile* (Müller) to the Shelligan Burn. Only 1.6 % of the spring fauna and 1.5 % of the June fauna of the Shelligan Burn belonged to species not present in the River Almond.

Each month the dry weight (24 hrs at 100°C) of the bottom fauna samples from the Shelligan Burn was 1.90 to 5.67 times greater than the dry weight of the samples from the River Almond. In the 90 samples taken in each stream from April to December 1962 there were 24,930 animals (weighing 6.466 g) in those from the Shelligan Burn compared with 9,167 animals (weighing 1.936 g) in those from the River Almond. By comparing the weight of animals caught by the sampling method used in this work with the weight of animals caught using a Surber sampler (Egglishaw and Mackay, in press) the mean standing stocks of bottom fauna (April 1962–April 1963) were estimated as 2.88 g dry weight per m² for the Shelligan Burn and 0.93 g dry weight per m² for the River Almond.

Thus, with the exception of one or two obvious differences seen in Table 2, the percentage compositions of the bottom fauna of the two streams have much in common. The density of the bottom fauna in the Shelligan Burn, however, is about three times greater than that in the River Almond. This probably results from the Shelligan Burn being chemically richer (Table 1) and containing a greater amount of allochthonic plant detritus, on which many of the bottom fauna organisms feed, than the River Almond (Egglishaw 1964, 1965). In the

Shelligan Burn in 1962 there was, per sample, an average of 5.4 ml of plant detritus in April, 7.6 ml in June, 15.6 ml in July, 11.1 ml in August, and about 7 ml in September, October and November. In the River Almond the amounts were 5.0 ml in April and between 2.2 ml and 4.4 ml in the other months.

THE SALMON AND TROUT POPULATIONS OF THE TWO STREAMS

All fish were caught with the use of electric stunning apparatus. From February 1962 until August 1963 a small portable battery-driven model was used, but after this, apparatus was used which had a 500 W generator driven by a 50 cc. petrol-engine as a power source. The technique of electric fishing is now generally considered to be the best method of obtaining fish for stomach analyses. With good apparatus a sample of fish can usually be caught within a short period of time, the apparatus can catch fish from all habitats of a stream and it does not select fish on the basis of their feeding behaviour or their readiness to take food. Fish caught for feeding studies are thus more representative of the population of fish of similar size than are fish caught by methods such as angling and netting.

During the period the battery stunner was used, all fish caught were preserved. Attempts were made to obtain a sample of about seven or more fish of each age class of both salmon and trout each month from both the Shelligan Burn and the River Almond. This was only partly successful, and for some months a smaller sample or none was obtained. During January and February 1963 the site on the River Almond was inaccessible due to heavy snowfall and so no fish were obtained from this stream at this time. That only small samples were obtained at other times was due to the poor stunning efficiency of the battery apparatus in conditions of low temperature or fast-flowing water, and the fact that the charge in the battery lasted only about one hour of fishing time. At other times the apparatus broke down and could not be repaired in the field. The petrol-engine apparatus caught many more fish more quickly and only those required for analyses of their stomach contents were preserved, the lengths of the rest being measured before they were released.

All lengths were measured from the tip of the jaws to the fork of the tail and the wet weight of each fish whose stomach contents were examined was also determined.

As the fish were kept in formaldehyde the affect of this preservative on the length and wet weight of fish was examined. Ten salmon and ten trout of various sizes were measured immediately after killing and then at intervals after being preserved in 4 % formaldehyde. There was no effect on the length of the fish but after immersion in formaldehyde for seven days the fish weighed between 4.5 and 12.9 % more than their fresh weight, the mean increase in weight being 8.7 %. After 14 days in preservative the fish were on average 7.9 % heavier than their fresh weight, 15 of the 20 fish having lost weight during the second seven days in preservative. The fish continued to lose weight and after ten weeks in preservative the average increase had fallen to 7.0 % of their fresh weight. They remained at this weight for the following year. No differences were found in the relative increases in weight between salmon and trout or between large and smaller fish. The weights of fish given in this account are the weights of fish that have been three to six months in preservative after excess preservative had been removed with a cloth or filter paper.

(a) GROWTH OF THE SALMON AND TROUT

The smallest salmon and trout found to be feeding were caught in May. April 1st or later has therefore been considered as the date on which they emerge from the substrate and their first year of life therefore extends to 31st March of the following year. Fish throughout this period are referred to as 0 + fish. Fish in subsequent years of their life are referred to as 1 +, 2 +, etc. fish.

The mean length and the range in length of the different year classes of salmon and trout caught in the Shelligan Burn are shown in Fig. 1 and similar data concerning fish from the River Almond are shown in Fig. 2. The numbers of fish on which the measurements are based are given in Figs. 5 and 6. Some larger trout which were caught are not included in Figs. 1 and 2. The ages of fish that were near the borderline of two size groups were determined from a microscopic examination of their scales.

Several workers (e.g. Allen (1940, 1941b) Frost (1950) on salmon; Frost (1950) Horton (1961) on trout) have made measurements of the length and weight of the fish caught at a site in a stream at intervals and referred to the increase in these measurements as 'growth', and from this have calculated growth rates. However, due to the movements of salmon and trout which are known to occur (Stuart, 1957) calculations of growth

rates from measurements of fish at a site in a stream must be treated with caution. It seems very probable that an area of stream that is suitable for a certain number of salmon or trout of a certain size range would become less suitable for particular fish as growth proceeds and that, consequently, the population of fish moving from the area would deviate with regard to size from the population remaining in the area. Thus, in stretches of the stream where the stones are small and the water shallow, large salmon or trout are rarely found, so as fish grow they must move out of these stretches.

That changes in the average size of salmon or trout at a site can be due to changes of the population rather

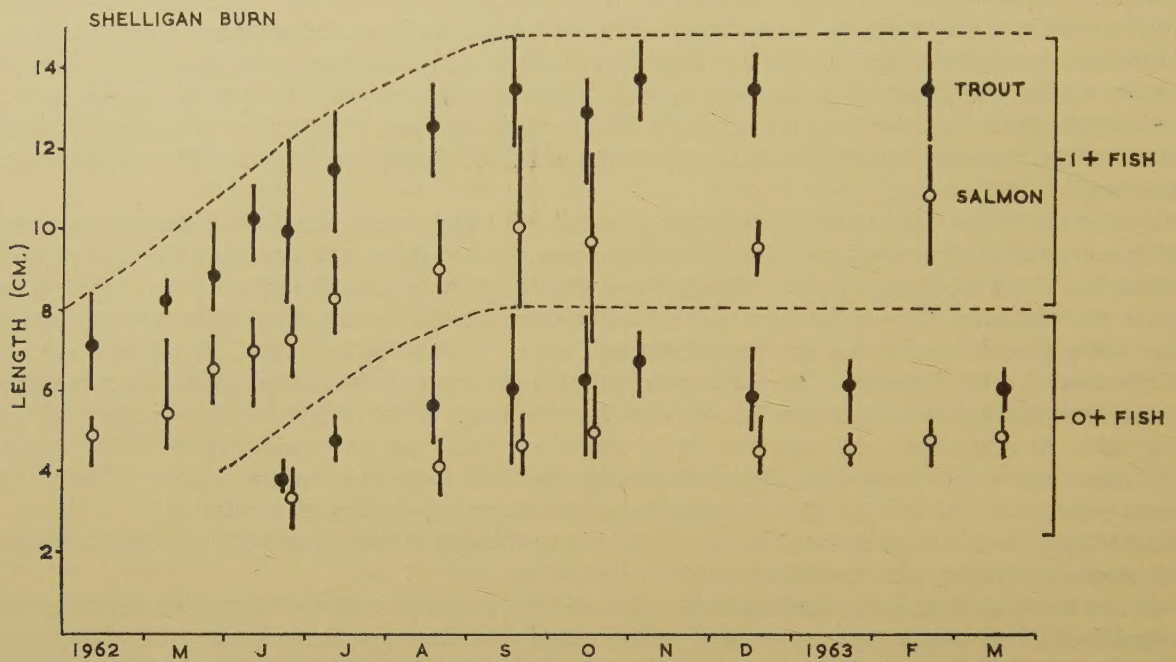


Fig. 1. The mean length and range in length of salmon and trout from the Shelligan Burn.

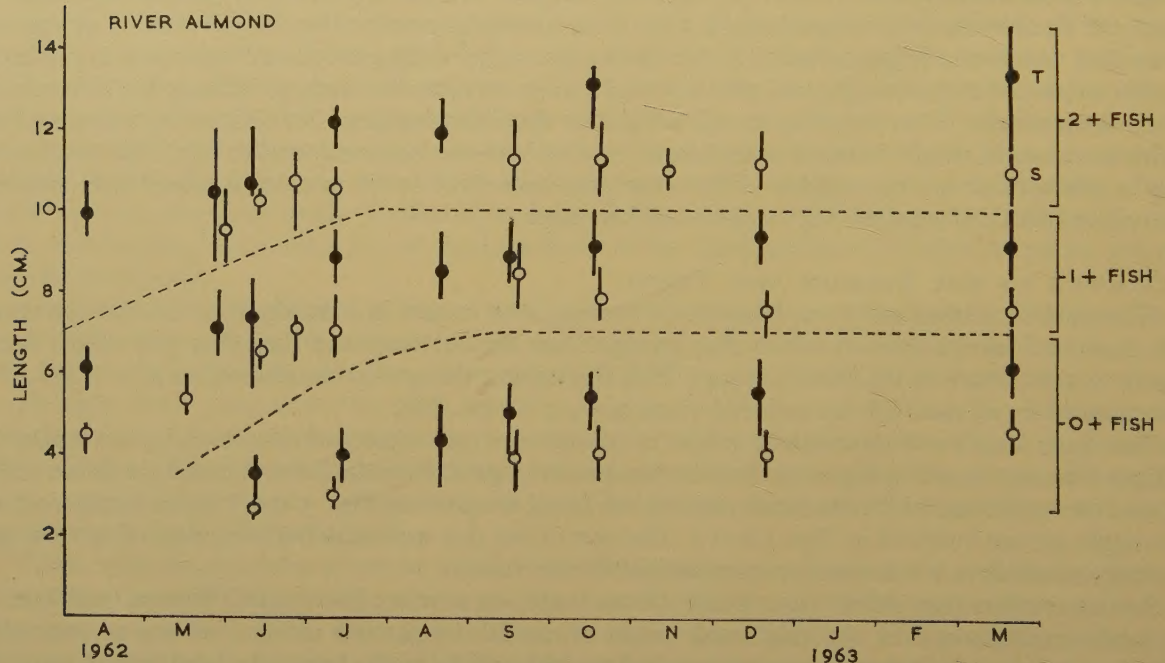


Fig. 2 The mean length and range in length of salmon and trout from the River Almond,

than changes in growth of the 'resident' population was shown by removing, and releasing downstream, the fish in an area of the Shelligan Burn and discovering what population recolonised the area within two weeks. It was estimated that 96 % of the fish originally present were removed. The results appear in Table 3.

It can be seen that the area was colonised by smaller 0 + salmon than were present a fortnight previously, but the size of the 0 + trout was much the same as previously. At the time of the second electric fishing the stream water was much deeper and faster than on the first occasion. The electrical conductivity of the water was 55 micromhos/cm³ as against 69 micromhos/cm³ (at 20°C). It may be that the increased velocity of the water current gave fewer places of shelter for the smaller salmon and that therefore they generally drifted downstream or the smaller salmon may, in general, have to move about more for feeding than the larger fish due to competition for feeding stations (p. 23) and that, when the opportunity came for them to recolonise available feeding stations, they did so.

The areas of the Shelligan Burn and the River Almond selected for studying were large enough to include the variety of habitats of runs and pools found in these streams. This should help to avoid or reduce some sources of error when calculations of 'growth' are determined from fish caught in a more homogeneous environment.

Figs. 1 and 2 show that the pattern of increase in the average length of salmon caught in the Shelligan Burn and the River Almond is similar to the pattern found in the River Eden, Cumberland and Westmorland (Allen, 1940) and in three tributaries of the Thurso River, Caithness (Allen, 1941b) with the most rapid increase in May, June and July, less in April and August and September, and no increase from October to March. This pattern of increase in length seems also to apply to the trout of both the Shelligan Burn and the River Almond.

Salmon in the Shelligan Burn reach a length of 47 ± 7.1 mm (mean and standard deviation of fish caught October-December; mean weight 1.151 g) in their first year and 96 ± 11.2 mm (mean weight 10.643 g) in their second year. The trout in the Shelligan burn 'grow' faster than the salmon and attain a length of 62 ± 8.8 mm (2.836 g) in their first year and 130 ± 8.6 mm (28.446 g) in their second year.

The salmon and trout of the River Almond 'grow' at a slower rate than those in the Shelligan Burn, the trout again 'growing' faster than the salmon. Salmon reach a mean length of 43 mm (0.78 g) in their first year, 77 mm (4.77 g) in their second year, and 109 mm (16.25 g) in their third year; the respective measurements for trout are 55 mm (1.90 g), 92 mm (9.42 g) and 133 mm (27.36 g).

Salmon of 2 + years (95-123 mm in length) were present in the Shelligan Burn in April, May and June of each year they were studied (1962 and 1963) but few were caught during the following months suggesting the majority had migrated downstream into the main river. In the River Almond 2 + salmon were present throughout the year and 3 + salmon (112-134 mm in length) were present in April, May and June after which they were less common.

From Fig. 1 it can be seen that throughout the year in the Shelligan Burn the size range of the 1 + salmon is between the size ranges of the 0 + and 1 + trout, and that the size range of the 0 + trout is between those of the 0 + and 1 + salmon. Similar alternate spacing of the age classes of the salmon and trout are seen in the River Almond (Fig. 2). The length frequency distributions of salmon and trout from two areas of the Shelligan Burn from which attempts were made to catch all the fish present are given in Fig. 3. It was estimated that 96 % of the fish were caught, all but a few of which were measured. It can be seen that 0 + trout were more variable in size than the 0 + salmon, the coefficients of variability being 40.5 % for the trout and 34.3 % for the salmon.

Alternate spacing of the age classes of salmon and trout in the size frequency distribution of fish from an area of stream could possibly arise without interaction between the species but it seems more probable that it results from their competition for feeding stations. This is discussed later (p. 23).

(b) DENSITY OF THE FISH POPULATIONS

The numerical densities of the salmon and trout populations were determined in sections of the Shelligan Burn and River Almond isolated by stop-nets. Due to the large width of the River Almond it was practicable to place the nets only half-way across the stream and determine the number of fish within this half. Areas isolated were between 59 m² and 101 m². The density estimations were made in two ways—from captures in successive periods (Menhinnick, 1963) and by 'mark and recapture' (Petersen method).

The larger (1 + and older) fish were more vulnerable to the electric fishing than the 0 + fish. Under the conditions in which the fishing was carried out the probability of capture of the 1 + and larger fish in a fishing period was 85–90 % compared with about 50 % for the 0 + fish. Thus after two periods of about 40 minutes of electric fishing the isolated areas, all 1 + and larger fish had been caught, and after four periods of fishing about 94 % of the 0 + fish had been caught. As the probability of capture depends on the care taken to catch fish, the electrical conductivity and speed of flow of the water, the probability of capture of 0 + salmon and trout was calculated for each occasion and stream before the populations were determined. In the 'mark and recapture' method of estimating the populations, fish caught in the first period of electric fishing were dyed by immersion in a dilute solution of Bismark Brown Y (Deacon, 1961) and returned to the populations. Estimations by this method gave results identical with those from the first method for 1 + and older fish, and were within 4 % of the first method estimates for 0 + salmon and trout.

The results of these density estimations are given in Fig. 4. The lengths of all fish caught were measured

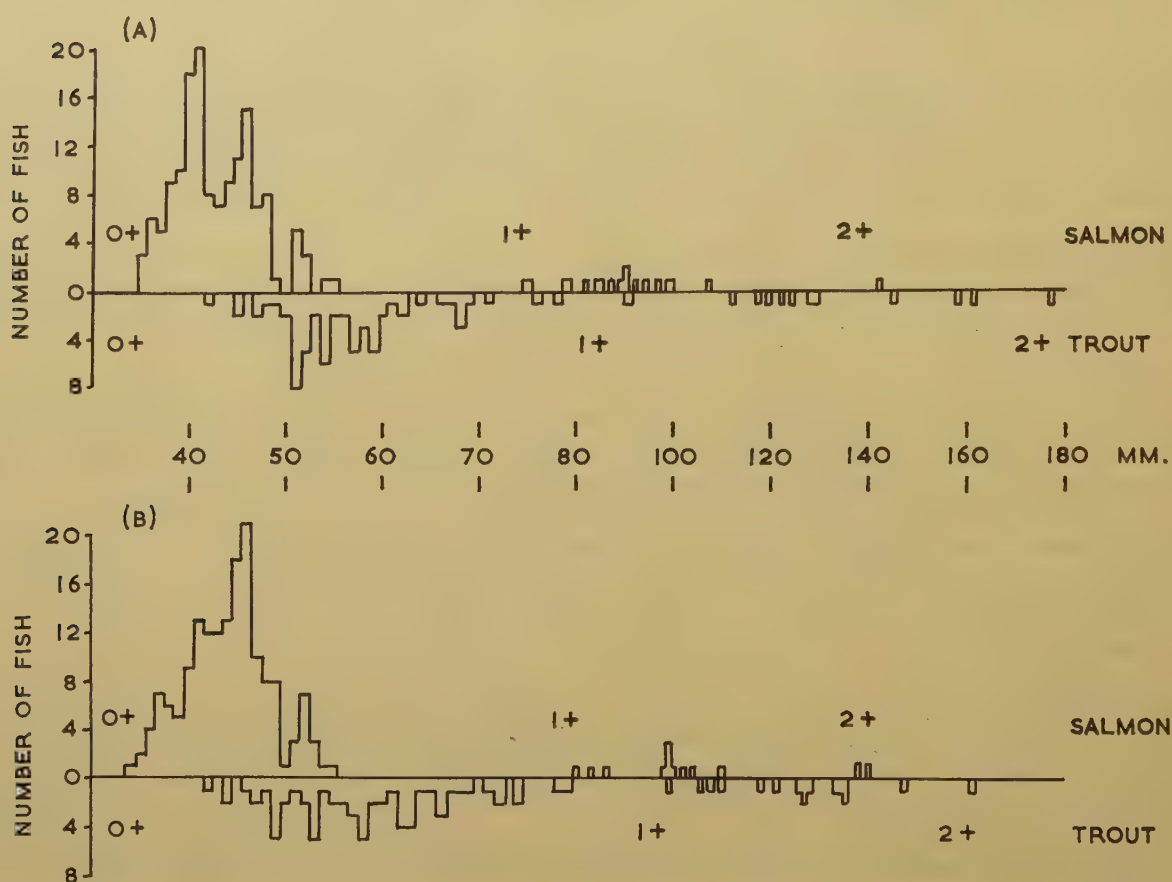


Fig. 3. The length frequency distributions of salmon (placed above the base line of each graph) and trout (placed below the base line) caught in two isolated stretches of the Shelligan Burn, (A) 15 October, 1963, area 69 m², (B) 9 October, 1963 area 59 m². Note scale of length of fish changes at 80 mm.

before the fish were returned to the stream, and from these lengths the weights of the fish were read from a graph relating known weights and lengths of fish. The results given in the figure are the numbers and estimated weights of each age class of salmon and trout per m² of stream isolated. Unfortunately, precisely comparable data between the River Almond and Shelligan Burn are relatively few.

The results indicate that in the Shelligan Burn the numerical density of 0 + salmon is probably two to three times that of the 0 + trout at the end of the growth period, and that the numerical densities of 1 + and

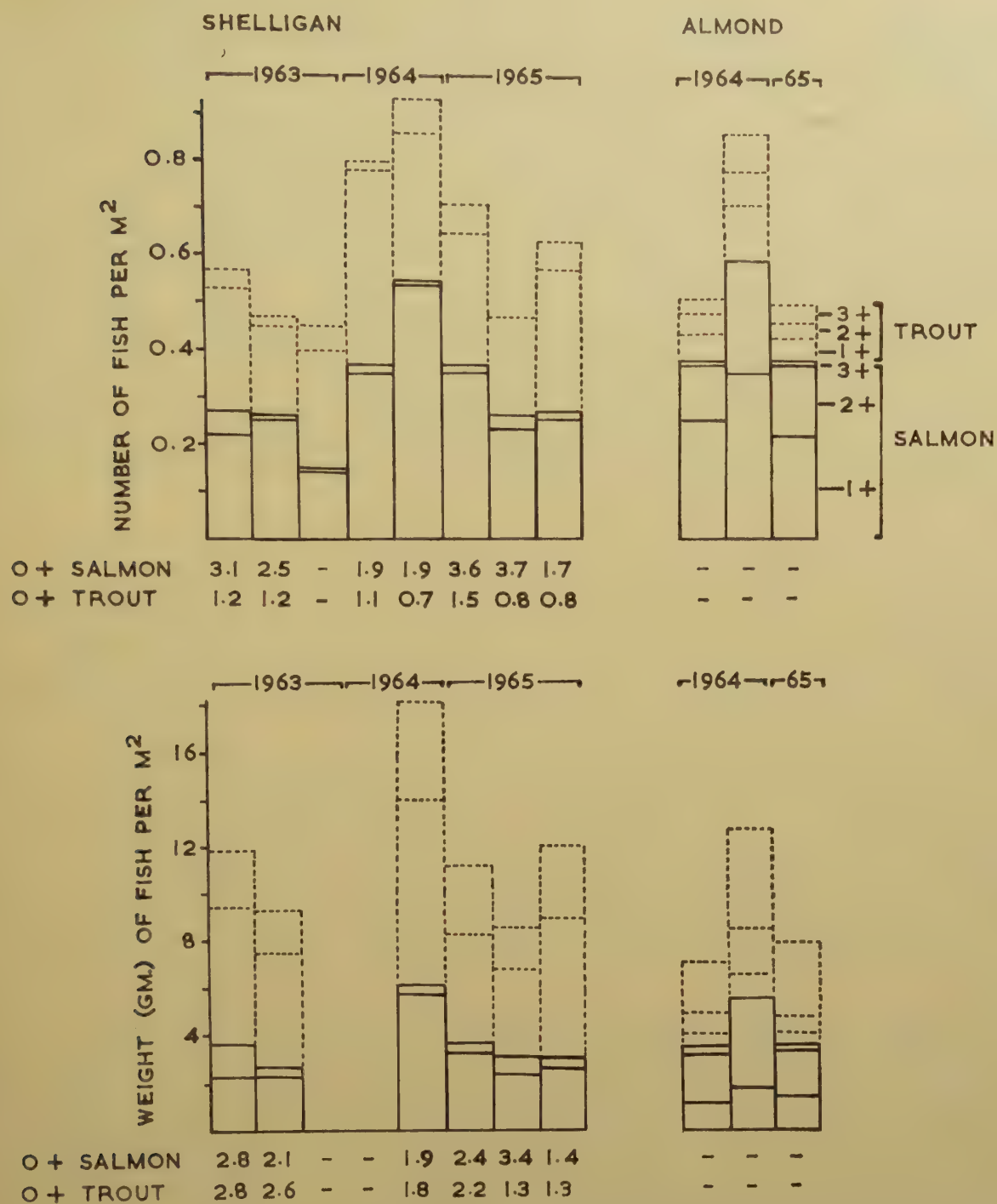


Fig. 4. Population densities of young salmon and trout in sections of the Shelligan Burn and River Almond. The histograms show the population densities of 1+ and older fish; data for 0+ fish are fewer and, where available, are given below each histogram.

2 + salmon and trout are about equal. Because of the larger sizes of the trout the biomass density of the 0 + salmon is similar to that of the 0 + trout, and there is a greater biomass density of both 1 + and 2 + trout than salmon of these ages in the Shelligan Burn. In the River Almond the numerical density of 1 + and 2 + salmon is higher than that of the trout as is their overall weight, although the weights (and numbers) of 3 + trout greatly exceed those of salmon, presumably the result of migration.

The numerical density of 1 + salmon is probably greater in the Shelligan Burn than in the River Almond, while 2 + salmon are more dense in the River Almond and there are also some 3 + salmon in this stream and none in the Shelligan Burn, again suggesting the possibility of migration. The biomass of salmon per unit area is probably similar in the two streams, although comparative data are inadequate. The numerical density of 1 + and older trout in the River Almond is about half of that for the Shelligan Burn. Both the numerical density and biomass density of the total of 1 + and older salmon and trout are probably not a great deal less in the River Almond than in the Shelligan Burn.

Few figures of population densities of salmon and trout in streams have appeared in the literature. Those available are less than comparable figures for the Shelligan Burn and River Almond. Mills (1964, p. 16 and Table 7) dealing with salmon of 1 + and older, gives five indices (= numerical densities) of between 0.05/m² and 0.08/m² and one of 0.18/m² for sections of the River Bran and its tributaries, 0.08/m² for the River Blackwater and 0.01/m² for the River Meig. Le Cren (1958) found between 0.6 and 4 trout per m² in streams up to 2 m wide in Northern England. Horton (1961) gives six stock (= biomass) densities of between 0.83 g/m² and 1.92 g/m² for trout of all ages in sections of a Dartmoor stream during October.

THE FOOD OF THE FISH

When using the electrical stunning apparatus care was taken to work upstream when obtaining the sample of fish, to lessen the possibility of catching fish that may either have fed on bottom fauna dislodged by the workers or fed on organisms that had become easier to catch due to the effect of the electric shocking. It was noticed that the petrol-driven apparatus often affected the behaviour of the larger Oligochaeta and Plecoptera, causing them to leave the substrate and drift downstream.

Salmon and trout feed by ingesting whole animals, mainly invertebrates but occasionally small fish. The state of the food in the cardiac portion of the stomach was usually almost as it had been caught; sometimes the organisms were crushed and enveloped in white opaque material, but it was nearly always possible to identify the organisms and measure their lengths. The contents of the pyloric portion of the stomach comprised organisms in various states of disintegration. It would have been difficult to identify, count and estimate the length of the constituent animals and no attempt was made to do so. The intestinal contents were mainly sclerotised fragments of invertebrates in a brown semi-liquid, all soft parts of the invertebrates having been dissolved. Some parts could often be recognised, such as the head capsules of Chironomidae, the mouthparts and segmental walls of Plecoptera and Ephemeroptera, and such parts as elytra and wings of terrestrial insects.

Only the contents of the cardiac portion of the stomach and the contents of the oesophagus were examined entirely, each organism present was identified as far as practicable and its length measured to the nearest mm. In the following account the term 'stomach contents' refers to the contents of the cardiac portion of the stomach (where nearly all the organisms were found) and the oesophagus only. The dry weights (24 hrs at 100°C) of all the common bottom fauna species of different lengths were determined from collections of animals from the streams, so that the dry weight of the total stomach contents of each fish could be calculated. Horton (1961) also gives the weight of the contents of salmon and trout stomachs from summed calculated weights of the constituent organisms.

The stomach contents of both salmon and trout included organisms of benthic origin taken either from the substrate or drifting in the current, organisms normally closely attached to stones (e.g. Hydroptilidae, Glossosomatinae and *Ancylastrum* spp.), animals moving away from the bottom to the surface of the water at times of emergence, animals living on the water surface (e.g. Dixinae, *Velia* spp.) and fauna of terrestrial origin attracted to the water surface, or washed or blown into the stream. They also feed at their own trophic level, taking salmon and trout eggs and smaller fish.

(a) THE VARIATION IN THE CONTENTS OF THE STOMACHS

Some previous workers (e.g. Allen (1940), Frost (1939, 1950), Horton (1961), Maitland (1965), McCormack (1962), Mills (1964)) who have examined and described the stomach contents of salmon and trout have presented their results as averages of the food in the several fish in a sample, without describing the variation found within samples. This omission might suggest that the amounts of food in stomachs were fairly symmetrically distributed about the mean and did not vary greatly but in the present work it was found that the variation was exceedingly large.

Table 4 indicates the wide variation found in the number and weight of invertebrates found in the stomachs of samples of ten or more salmon or trout taken from the Shelligan Burn in 1962. The variation found in the contents of samples of fish from the River Almond was also exceedingly large.

The numbers of certain food organisms in the stomachs of a sample of salmon or trout varied greatly. Allen (1941a) believed that, with increase in the number of animals in the stomachs of salmon, the degree of selection of food by the fish increased and that at least 80 % of salmon with more than ten animals in their stomachs appeared to be selecting their food. The selection of food by salmon and trout, with the corollary that some organisms suitable as food are ignored or ejected, seems unlikely to be a general behavioural procedure. The present writer considers that what is apparent selection of food (i.e. when there are relatively high numbers of particular food organisms present in stomachs) can often be, with more reason, attributed to the behaviour or distribution of certain benthic organisms, or the heterogeneity of the feeding environment of the fish population (p. 14).

Of the salmon and trout examined from February 1962 to March 1963 17 of 449 from the Shelligan Burn and 23 of 372 from the River Almond contained eight or more of the same species of bottom fauna. Details concerning these fish and the food organisms are given in Table 5. This table also includes six fish which contained eight or more of certain species of emerging or terrestrial fauna.

The organisms that occurred most frequently in large numbers in the stomachs of salmon and trout were *Hydroptila* spp., *Simulium* spp., *Baetis* spp. and *Leuctra* spp. (Table 5). *Hydroptila* spp. feed on algae on the upper surface of stones and *Simulium* spp. feed by extracting food particles from the current. Both *Hydroptila* spp. and *Simulium* spp. feed in more exposed situations than most other benthic organisms, which feed on plant detritus beneath stones and gravel, and they can be densely aggregated at certain sites (Egglishaw, 1964) where other organisms are sparse. It seems more likely that this distribution could account for the presence of large numbers of *Hydroptila* spp. and *Simulium* spp. in certain fish than that the fish selected these organisms from among those available to them.

Unlike the populations of *Hydroptila* spp. and *Simulium* spp., the populations of *Baetis* spp. and *Leuctra* spp. and most other benthic species, are more interspersed with other species. When salmon and trout contain large numbers of one of these species there is usually a considerable number of other organisms present (Table 5), suggesting the species present in large numbers was not selected. In addition, *Baetis* spp. are among the most free-swimming of benthic organisms occurring frequently in the 'drift fauna' and this would increase their availability to salmon and trout.

The particular distribution of some species can probably account for them being eaten less frequently than might be expected. Although *Chloroperla torrentium* is common in the Shelligan Burn in spring, making up 8 % of the number of animals collected in the samples in May, and has a higher average density than *Amphinemura sulciollis* (6 %) and *Isoperla grammica* (2 %) it is comparatively rarer in stomach contents, comprising only 1 % of the contents of 1 + salmon (see Table 8). Pentelov (1932) remarks that *Chloroperla torrentium*, although very common in bottom fauna collections from the River Tees, was not eaten by the trout present. *C. torrentium*, unlike most other Plecoptera, does not aggregate in plant detritus but is randomly distributed in riffles (Egglishaw, 1964). If the factors determining the optimal conditions for feeding by salmon and trout are related to some of the factors also determining the accumulation of plant detritus, then the aggregation of Plecoptera (*Leuctra*, *Amphinemura*, *Protonemura*, *Isoperla*) other than *C. torrentium* might account for the latter species being eaten less often than other Plecoptera when compared with their relative proportions in the bottom fauna. Ivlev (1961) using carp, roach and bleak, has shown experimentally that a patchiness in the distribution of a food material increases the quantity of food consumed in a given time, by comparison with an even food distribution, when the average concentration is the same in both cases.

(b) THE FOOD OF FISH FROM DIFFERENT HABITATS OF THE SAME STREAM

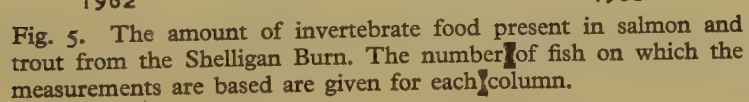
Attempts were made to discover in what ways heterogeneity of the fishes' physical environment, with consequent differences in the food available at different sites, affected the variation in the stomach contents. Several workers have observed that salmon and trout can spend much of their time at a feeding station from which they make short feeding excursions and Kalleberg (1958) has studied this behaviour in a large stream tank. The kind and amount of food at or drifting to a feeding station in streams such as the Shelligan Burn and River Almond will depend on several factors among which will be the density of the bottom fauna present on the stream substrate and in the water, the volume of water passing through the feeding station, the relationship of the feeding station to sources of terrestrial food and the distribution of other feeding stations upstream. Samples of salmon and trout were caught with the electrical stunning machine from what were considered to be the most dissimilar habitats in the sections of the Shelligan Burn and River Almond studied. A comparison of the stomach contents of the fish from the different habitats of each stream is given in Table 6. Only 0.1 % of the organisms found in the stomachs are not included in the table.

From the Shelligan Burn salmon and trout were caught in 'pools' of slow-running water, 30–38 cm deep, and in two 'runs' of faster water, 8–16 cm deep. All the fish were caught within a 140 m stretch of the stream. There was no significant difference in the kind or amount of food in the stomachs of both the trout and the salmon of the two runs, although, as can be seen from Table 6, there were considerable differences between the food, particularly that of terrestrial origin, of the salmon and that of the trout. However, the 1 + trout from the pools contained significantly more terrestrial organisms (a mean of 57.6 compared with 6.5, $P = .05$, and with 11.7, $P = .05-.02$) and less emerging *Baetis* spp. (a mean of 0.1 compared with 2.5, $P = .1-.05$, and with 3.1, $P = .02-.01$) than 1 + trout from the two runs. The 1 + salmon from the pools also contained significantly more terrestrial organisms than the 1 + salmon from one of the runs ($6.5 > 0.5$, $P = .02-.01$). An inadequate sample of salmon was caught in the second run.

From the River Almond salmon were caught in a pool of slow-running water, mainly about 25 cm deep but in places reaching 46 cm, and in runs of faster water, 8–20 cm deep. An inadequate number of trout was obtained from the runs but the stomach contents of the sample from the pool is included in Table 6. Of the benthic organisms the salmon in the pool fed less on *Baetis* ($0.1 < 1.1$, $P < .01$) and more on chironomid pupae ($2.5 > 0.0$, $P < .01$) than salmon of equivalent size from runs. *Baetis* spp. are relatively less common in the slowest parts of streams than they are in runs. The differences in the mean numbers of *Hydroptila* spp. present were not significant; there was great variation in the numbers present in the fish from both the pool and the runs. The most important difference in the stomach contents of the salmon from the pool and runs was in their number of emerging Chironomidae ($14.1 > 0.0$, $P < .01$). The salmon from the pool also contained more terrestrial organisms than salmon from the runs ($4.8 > 0.1$, $P < .01$).

The food of the salmon in the pool is, in certain ways, more similar to that of the trout in the pool than that of the salmon in the runs. These similarities, such as the small numbers of *Baetis* spp. and the large numbers of emerging Chironomidae and terrestrial fauna compared with the food eaten by the fish in the runs, must be due to the physical nature of the pool and runs. It is apparent that salmon and trout in pools feed more at the water surface than they do in runs. This presumably is due to several reasons, among which may be the less turbulent conditions in pools allowing the fish to regain shelter more easily, the accumulation of terrestrial organisms on the surface of pools, because of the slower current speed and also because the organisms are more easily seen in the less turbulent water. However, even from the pool the salmon, compared with the trout, contained more of certain benthic organisms (*Hydroptila* spp. $44.2 > 8.6$, $P < .01$; chironomid larvae $8.8 > 0.7$, $P < .01$) and less terrestrial fauna ($4.8 < 10.9$, $P = .05-.02$). These differences are more likely to be due to differences in the food available to the salmon and the trout, because of their different feeding positions and habits rather than due to the salmon and trout selecting different food organisms from among those available. The emerging Chironomidae were probably caught moving from the bottom of the pool to the water surface, rather than caught at the water surface after having drifted into the pool from upstream. If they had been caught at the surface they might be expected to be present in both salmon and trout in the same proportions as the other surface food, the terrestrial fauna.

During work on the feeding by salmon and trout on salmonid eggs (p. 20) it was found that there could be large differences in the number of eggs in the stomach contents of fish caught at different sites. On the first date of the 1963 spawning that fish were found with salmonid eggs among their stomach contents, samples



RIVER ALMOND

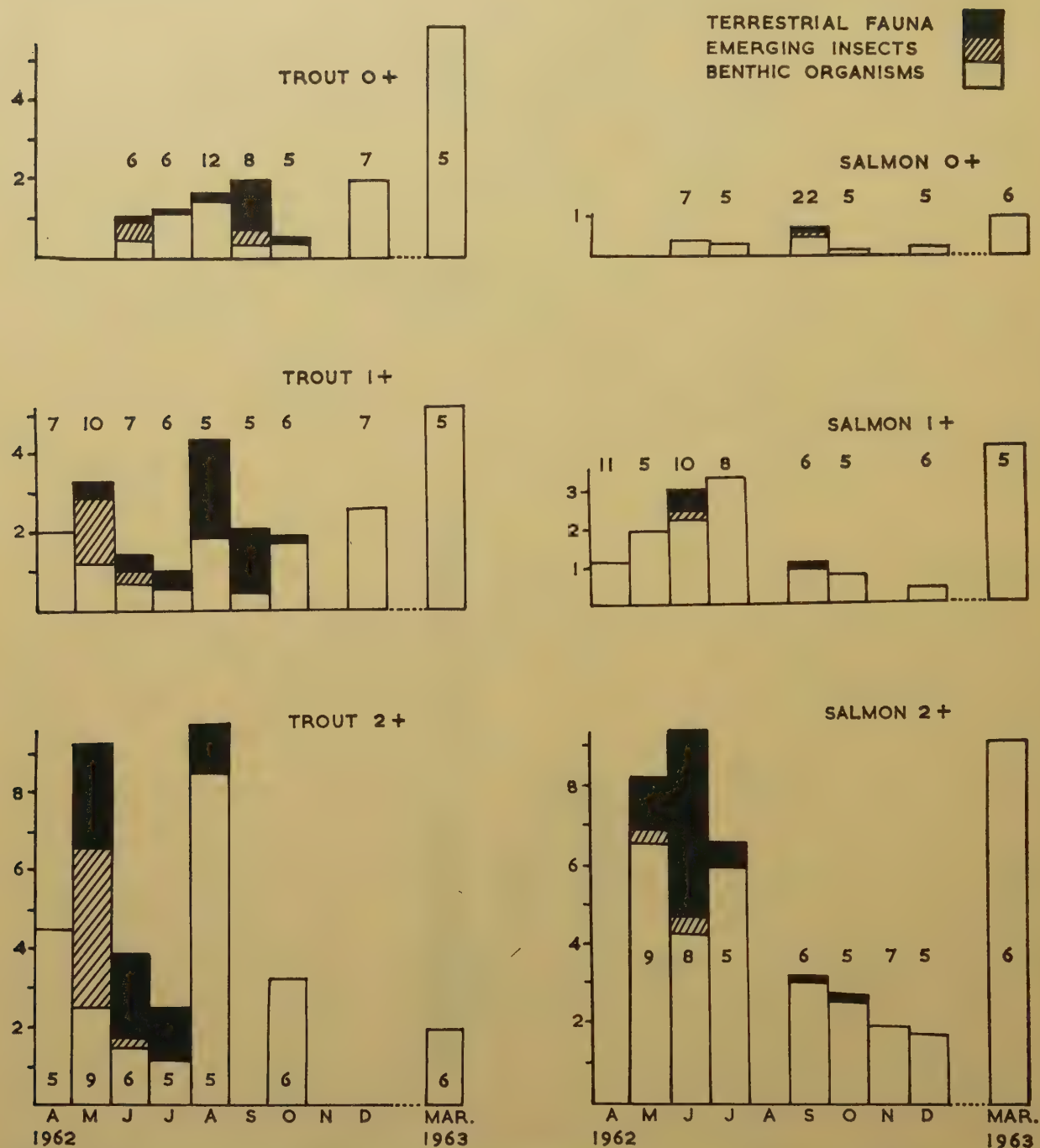


Fig. 6. The amount of invertebrate food present in salmon and trout from the River Almond. The number of fish on which the measurements are based are given for each column.

of fish were caught at seven sites in the Shelligan Burn. The seven sites were classed as either pools or runs and all were situated within a 120 m stretch of the stream. In the most upstream site examined, a run, nine of eleven trout over 90 mm in length contained salmonid eggs in their stomachs, the mean number of eggs per trout being 8.6. From a pool below this run, eight of ten trout over 90 mm long which were caught contained salmonid eggs (mean number of 15.9 per trout). From another pool, downstream from the last one, two of five trout caught contained salmonid eggs in their stomachs. In the succeeding four sites, two runs and two pools, no trout of 36 over 90 mm long that were examined contained salmonid eggs.

(c) SEASONAL CHANGES IN THE FOOD CONSUMED

(i) *The amount of food present in the stomachs*

The amounts of invertebrate food present in the stomachs of fish in the Shelligan Burn and River Almond throughout the year are given in Figs. 5 and 6. The food has been divided into three classes; benthic animals, emerging insects and fauna of terrestrial origin. Because of the considerable variation in stomach contents previously mentioned and the relative smallness of the samples of fish, it might be misleading to make a finer classification than this for these histograms. Details of species of food organisms taken in some months are given later. In addition to the invertebrate food in the stomachs of the fish, there were occasionally small fish (p. 22) and salmon and trout eggs (p. 21). The amounts of these have not been included in Figs. 5 and 6.

The terrestrial fauna includes, as well as the invertebrates which bred on the surrounding land and which were blown, washed or attracted into the streams, a very small number of insects which live and feed on the surface of the water (e.g. *Velia* spp., larvae of Dixinae, possibly some Collembola) and also the aerial stages of insects whose young stages are aquatic. The relative numbers of the animals comprising this terrestrial food are given below.

It is apparent that there is less food in the stomachs of both trout and salmon during the colder months of the year, November to February, than there is during the warmer months. Also, during November to April the stomachs of 18 % of the fish in the Shelligan Burn and 10 % of the fish in the River Almond contained no invertebrate food, whilst during May to October only 5 % of the fish in the Shelligan Burn and 4 % of the fish in the River Almond contained no invertebrate food. Thomas (1962), from the analysis of trout and salmon stomach contents, concluded that these fish in the River Teify feed actively at all seasons regardless of temperature. Stomach contents, however, give little indication of the rate of feeding because the rate of digestion is related to temperature. At low temperatures the rate of digestion is extremely slow, and food may remain in the stomach for several days (p. 20). In this respect the histograms (Figs. 5 and 6) give a very conservative indication of the relative amounts of food consumed each month. The amounts consumed in the summer months compared with the amounts consumed in the colder months would probably be several times larger (probably three times, using figures for roach given by Nikolsky (1963)) than the relative amounts of food in the stomachs at these times.

Thomas (1962, Fig. 5) showed that the number of trout growing rapidly, as indicated by wide circuli in the outer annulus of the scales, fell quickly during September, and that less than 10 % of trout showed rapid growth during the period November to February, even though they had as full stomachs during this period as they had during summer (Thomas, l.c. Table 2). The slow growth or absence of growth of trout and salmon which has generally been observed in British waters during winter (e.g. Allen (1940, 1941b), Horton (1961, Thomas (1962)) would seem to be due to a physiological loss in capacity of the alimentary system to digest food, and little to do with the availability of bottom fauna and other food at this time. No significant decrease in the quantity of bottom fauna, and particularly that part eaten by the fish, was found in the Shelligan Burn or River Almond during late summer through to winter (Egglishaw and Mackay, in press).

(ii) *Food of terrestrial origin*

As the vegetation surrounding the Shelligan Burn is much richer and more varied than that surrounding the River Almond, one might expect the salmon and trout from the Shelligan Burn to contain more terrestrial organisms than fish from the River Almond. Table 7 shows that whilst there was usually (eight of eleven comparisons) a greater weight of terrestrial food, there were usually fewer (nine of eleven comparisons) terrestrial organisms, in fish from the Shelligan Burn than in fish from the River Almond.

The terrestrial food organisms were separated into 26 taxonomic categories, representatives of 24 of which were found in fish from the Shelligan Burn, and representatives of 16 were found in fish from the River Almond. Some of the categories included a large number of species.

The commonest organisms eaten by salmon and trout in each stream were adults of Hymenoptera, Diptera and Hemiptera (together comprising 49 % of the terrestrial organisms in fish from the Shelligan Burn, and 80 % in fish from the River Almond and the majority being 1–3 mm long), Coleoptera (8 % in fish from the Shelligan Burn and 8 % in fish from the River Almond) and Collembola (8 % and 3 %). The relatively larger and less sclerotised terrestrial organisms, larvae of Diptera (about 10 mm long, 17 %), larvae of Lepidoptera (between 12 mm and 30 mm in length, 3 %) and Araneida (3 %) were present in fish from the Shelligan Burn, but these groups comprised only 0.4 % of the terrestrial organisms in fish from the River Almond. Only 6 % of the terrestrial organisms in fish from the Shelligan Burn, and 6 % in fish from the River Almond were adults of insects having aquatic larvae.

The increase in the amount of terrestrial food in salmon and trout in the Shelligan Burn in October (Fig. 5) was probably due to a large quantity of terrestrial organisms being washed into the stream as a result of heavy rainfall during the week before the samples of fish were caught. It is possible that, on other occasions, apparent seasonal changes in food taken by salmon and trout are the result of particular weather conditions.

Emerging insects were caught more by trout than salmon in both streams. Most emerging insects caught were taken during May to August, and were chiefly Chironomidae and Trichoptera, with smaller numbers of *Baetis* spp., Ecdyonuridae, *Ephemerella ignita* and Plecoptera.

(iii) Benthic food

Due to the various life-histories of the component species, the composition of the bottom fauna of streams is constantly changing throughout the year in respect of the sizes, developmental stages and kinds of organisms present. Seasonal changes in the composition of the benthic food of salmon and trout are given by Horton (1961) for trout in a Dartmoor stream, by Thomas (1962) for both salmon and trout in the River Teify and by Maitland (1965) for salmon and trout in the River Endrick. Only a short account of this subject is required here.

The samples of bottom fauna which were taken from the Shelligan Burn and the River Almond give a fair indication of the food available to the fish. There is no collecting method that would sample all components of the bottom fauna with equal accuracy, all methods being selective in some way. The method used (p. 6) collects the more freely-moving animals, but animals that cling to stones are not so well sampled. The composition by number of the bottom fauna samples and the benthic food of salmon and trout on certain occasions when the largest fish samples were obtained are shown in Table 8. There are certain fairly consistent differences between the fauna sampled by the net and that eaten by the fish. Relative to other benthic organisms the net catches more total Ephemeroptera and *Baetis* spp. and fewer Chironomidae and *Hydroptila* spp. than are eaten by the salmon and trout.

From the beginning of the year to May, Plecoptera, particularly *Leuctra inermis* and *Amphinemura sulcicollis*, made up a large proportion of the stomach contents of salmon and trout in the Shelligan Burn. In May itself Plecoptera formed 28 % by number and 36 % by weight of the benthic food of 1 + salmon and 53 % by number and 42 % by weight of the benthic food of 1 + trout.

Most of the winter-growing Plecoptera emerged from the Shelligan Burn and River Almond before the end of May and so the plecopteran contribution to the food of fish in June decreased. In June Plecoptera comprised 6 % of the number and 20 % of the weight of benthic food organisms of 1 + salmon and 2 % of the number and 2 % of the weight of benthic food organisms of 1 + trout. In spring the *Leuctra* (Table 8) were nearly all *L. inermis* and from June to August the *Leuctra* were nearly all *L. fusca*, this species comprising just less than one half of the plecopteran fauna in June and about three-quarters of it in July and August. In September the winter-growing Plecoptera begin to hatch and again begin to comprise a large part of the bottom fauna.

Ephemeroptera always comprised a large proportion of the food of salmon and trout throughout the year in both streams. In winter and spring the *Baetis* population in both streams was *B. rhodani* with a small number of *B. pumilus*, and during summer the *Baetis* population was *B. scambus* or *B. bioculatus* and *B. vernus* or *B. tenax*. The percentage weight of *Baetis* spp. in the benthic food of 1 + salmon from the Shelligan Burn was 8 %, 12 % and 7 %, and for 1 + trout was 7 %, 2 % and 4 % in May, June and August respectively. Compared with the Shelligan Burn there was, in June, a relatively greater amount of *Baetis* in both the bottom fauna and

in the stomach contents of salmon and trout from the River Almond. The other Ephemeroptera present in both streams were species of Ecdyonuridae and, in June, July and August *Ephemerella ignita* comprised between 3 % and 11 % of the weight of benthic food in the stomachs of 1 % salmon and trout in the Shelligan Burn.

Species of *Hydroptila* were the Trichoptera most frequently eaten by salmon and trout in both streams. They were present in the bottom fauna mainly from April to July but, as previously mentioned, were not collected efficiently by the bottom fauna sampling method used. In May *Hydroptila* spp. comprised 1 % of the weight of the benthic food in 1 + salmon and 1 % in 1 + trout from the Shelligan Burn, and 12 % of the weight of benthic food in 1 + salmon and 11 % in 1 + trout from the River Almond.

Other Trichoptera eaten by both salmon and trout in the Shelligan Burn and River Almond were *Rhyacophila* spp., *Hydropsyche* spp., Limnephilidae, Glossosomatinae and Polycentropidae. Limnephilidae and *Hydropsyche* spp. comprised a relatively smaller proportion of both the bottom fauna and stomach contents of fish of the River Almond than they did in the Shelligan Burn. Thomas (1962) found that *Brachycentrus subnubilus* Curtis (Sericostomatidae), which was very common in the bottom fauna, was one of the chief food organisms of the salmonids present in the River Teify, forming 42 % of the food of salmon and 28 % of the food of trout. Sericostomatidae are very rare in the Shelligan Burn and apparently absent from the River Almond.

Chironomid larvae were nearly always numerically important in the food of salmon and trout of the Shelligan Burn and the River Almond. Being small, however, their contribution to the weight of food was much less important. In May, June and July for example they comprised 5 %, 6 % and 4 % respectively of the weight of benthic food in 1 + salmon and 2 %, 8 % and 3 % respectively of the weight of benthic food of 1 + trout from the Shelligan Burn.

The majority of Coleoptera in the bottom fauna samples from both the Shelligan Burn and the River Almond were adults and larvae of four species of Helmidae, *Esolus parallelipedus* and *Helmis maugei* being the most abundant. These Coleoptera are found under stones and gravel and are often deeper in the substrate than other benthic organisms (Morgan and Egglisshaw, 1965). Consequently they are not often eaten by either salmon or trout. Larvae of *Oreodytes* (?) *rivalis* occurred in the stomachs of salmon and trout, particularly in fish from the Shelligan Burn in June, but they were rarely collected in the bottom fauna samples. The larvae live among algae on stones and are not washed off during collecting.

Some organisms which were, at times, common in the bottom fauna collections were rarely or never found in the stomach contents of the fish. Hydracarina were rarely found in salmon or trout stomachs. In laboratory tanks salmon often captured free-swimming Hydracarina but ejected them. The Hydracarina have a hard exoskeleton and many are armed with short stout spines. Thomas (1962) found that, though Hydracarina were numerous in the fauna, they occurred very infrequently in the stomachs of salmonids of the River Teify. Oligochaetes of the family Naididae were present in both the Shelligan Burn and the River Almond throughout the year but were most common during the summer. In August they comprised 9 % of the number of animals collected in the samples from the Shelligan Burn and 66 % of those from the River Almond; in September the respective percentages were 5 and 34. However, no Naididae were ever recognised among the stomach contents of salmon or trout. *Crenobia alpina* was present throughout the year in both streams, comprising up to 4 % of the number of animals collected from the Shelligan Burn and up to 3 % of the samples from the River Almond. No *C. alpina* were found in the stomachs of salmon or trout.

It will be apparent that the productivity of salmon and trout is greatly dependent, directly and indirectly, on the character of the stream's surroundings. During the period May to October, when food consumption is greatest, about 40 % of the weight of food of trout and about 6 % of the weight of food of salmon in the Shelligan Burn is terrestrial invertebrates, and throughout the year a large proportion of benthic organisms in the Shelligan Burn feed on allochthonic plant material (Egglisshaw, 1964).

(iv) *The size of benthic food organisms*

Due to the various life-histories of the benthic organisms the size-frequency distribution of animals collected in the samples changed during the year. The greatest change in the Shelligan Burn occurred between May and June. By the end of May the spring-emerging insects had left the stream and in June their offspring and the larvae which hatched from overwintering eggs comprised a large proportion of the bottom fauna. Consequently the bottom fauna changed from being composed of relatively large organisms in May (a mean number of 124 organisms per sample, comprising 43 % of the animals collected, were 5 mm or more in length)

to being composed chiefly of smaller organisms in June (a mean of 30 animals per sample, 11 % of the animals collected, being 5 mm or longer). The large size of the mesh of the collecting net used underestimated the numbers of 1 mm and 2 mm animals present in the stream.

The effect of this change in size-frequency distribution of benthic animals from May to June on the food of the fish is shown in Table 9, which gives the size frequency distribution of the benthic fauna and the benthic food organisms of salmon and trout during these months. The percentage of the total weight of food organisms of 1 + salmon and 1 + trout that each length size comprised has also been calculated. It can be seen that although there is a considerable increase in the number of smaller organisms (3 mm or less) eaten in June they still contribute only a small amount to the food consumed by salmon and trout. Animals of 5 mm and longer contribute 77 % or more of the weight of food of 1 + salmon and trout in both months, and of these animals those of 9 mm or longer contribute at least one third of the weight of food.

That larger salmon and trout, because of their wider gape, eat greater quantities of larger food organisms than do smaller fish has been noted by Thomas (1962). From Table 9 it can be seen that 0 + salmon did not contain organisms longer than 6 mm, and that 0 + trout did not contain organisms longer than 8 mm or 9 mm, but older and larger fish contained larger food organisms. It is shown below that only salmon and trout longer than 66 mm feed on salmonid eggs, which have a diameter of about 6 mm.

(v) *Feeding on salmonid eggs*

In December 1962 the stomachs of salmon and trout from the Shelligan Burn and River Almond contained salmonid eggs and it was decided that this aspect of the feeding habits of the fish should be investigated more fully in the Shelligan Burn the following year.

The first adult salmon arrived at the spawning sites of the Shelligan Burn in October. The main spawning took place during November and December. There were also a few sea trout spawning in the Shelligan Burn during this period. From a rough census of the adult salmon and sea trout present in the stream during the spawning time it is thought that no more than one-eighth of the spawning fish were sea trout. As far as is known the eggs of the two species cannot be differentiated, but it is likely that most of the eggs here described as salmonid eggs are eggs of the salmon.

When spawning, a female releases several thousand eggs and, depending on the site, some of these must get carried away by the water current. Presumably it is these eggs that are mostly eaten by salmon and trout. However, on occasions, the stomachs of salmon and trout contained partly developed as well as undeveloped eggs. The spawning behaviour of salmon and trout, described by Jones (1959) involves vigorous activity during which the substrate is much disturbed. The partly-developed eggs on which fish had been feeding might have been dislodged by fish spawning over a redd made earlier by other fish. Thomas (1962) did not find eggs in the stomachs of salmon or trout, but, infrequently, they were present in eels. As some stomachs were full of eggs, the eels had probably taken them from a redd.

Samples of salmon and trout were caught at about weekly intervals from 9th October 1963 until 16th January 1964 during which period it was considered all spawning had taken place. Eggs were first found in the stomachs of fish on 8th November and continued to be present in fish until 16th January. On 8th November the number of eggs present in fish depended greatly on the site on the Shelligan Burn at which the fish were caught (p. 14). From 19th November the number of eggs present in the stomachs of fish was less variable and not obviously dependent on the sites at which they were caught.

No eggs were found in stomachs of 0 + salmon or in 0 + trout below 66 mm in length presumably because their gape is not wide enough. 0 + trout of 66 mm or longer contained a mean number of two eggs during December. On 8th November 1 + trout contained a mean of three eggs (14 of 43 fish contained eggs). This increased to a mean of 15 eggs by 19th November (20 of 21 fish contained eggs) and remained at about this figure until 20th December when there was a mean of three eggs present. By 16th January there were no eggs present in the stomach contents of 1 + trout. All told, 158 1 + trout were examined for eggs. Only small samples of 2 + trout were obtained and they contained more eggs than the 1 + trout. Nine 2 + trout caught on 4th December contained a mean of 39 eggs. A 3 + trout of 320 mm length caught at this time contained 143 eggs. Salmon 1 + years old contained a mean of eight eggs from 19th November until 11th December.

The digestive processes at this time of the year are slow. From laboratory experiments, in which trout were fed trout eggs and then killed at intervals to examine their stomach contents, it was found that eggs may

remain in the cardiac portion of the stomach for six days when the water temperature is 4°C. Assuming that the rate of digestion in the field is similar, then, during the spawning period, an 0+ trout of at least 66 mm length consumes a mean of ten eggs, a 1+ trout a mean of 100 eggs, a 2+ trout a mean of 175 eggs and a 1+ salmon a mean of 50 eggs. A total of about 50 eggs was consumed by salmon and trout per m² of stream. As spawning takes place throughout the 1.6 km downstream from the area investigated and the stream is similar with regard to width, depth, current speed and areas of runs and pools throughout this length, this egg consumption may be generally applicable.

THE FOOD OF SALMON INTRODUCED INTO A STREAM

The stocking of freshwaters with young fish reared in hatcheries and other artificial conditions to augment natural populations is carried out all over the world. Whilst for many species of fish the practice has obvious importance, the planting of salmon fry (usually fish whose yolk-sacs have been absorbed and which are beginning to feed actively) in streams, remains, in most cases, of doubtful value. In 1961 an opportunity arose to study the feeding of salmon fry that had been introduced to a stream (Allt dos Mhuicarain, Ross-shire).

Allt dos Mhuicarain, a tributary of the River Bran, flows over granite through heather and grass moorland. As can be seen from Table 1 this stream is much poorer in calcium, magnesium and bicarbonate than is the Shelligan Burn. The bottom fauna too, is less dense in Allt dos Mhuicarain than it is in the Shelligan Burn at all seasons of the year (Egglishaw 1964, Egglishaw and Mackay, in press) the weight of organisms per sample being about five times greater in the Shelligan Burn.

In April 1960, 16,150 unfed salmon fry were added to 1060 m² of Allt dos Mhuicarain and the subsequent mortality of the fry was investigated by Mills (1964). He found that, by September 1960, 18 % of the planted fry had moved out of the stream through a trap sited near its mouth. The stream was electrically fished in September when 204 fry were found to be present. The mortality of the fry that remained in Allt dos Mhuicarain was thus 98.4 % (Mills, l.c.). In April 1961 a similar planting of fry resulted in a mortality of 99.6 %. Heavy mortalities of planted fry occurred in Allt dos Mhuicarain in the following years and in another stream studied (Mills (1964), Report on the Fisheries of Scotland for 1964, London, HMSO, p. 110).

To discover if the heavy mortality of fry was due to their starvation in the early period after planting, the present writer investigated their feeding, growth and condition and compared them with wild fry from the Shelligan Burn.

Samples of the stocked fry were collected from Allt dos Mhuicarain from the time the fry were introduced on 21st April 1961 until mid-June. The length and weight of 253 fry from this stream were measured and the gut contents of 165 of these were identified. One hundred and seventy natural fry, all collected from a 20 m stretch of the Shelligan Burn during the same period, were also examined.

Fry caught in the Shelligan Burn on 8th May had a mean weight of 138 mg and 10 out of 32 were feeding. The fry in Allt dos Mhuicarain (mean weight 133 mg when planted) had a mean weight of 138 mg on 27th April when 11 of 28 were feeding. Fourteen days after this stage of development, fry from the Shelligan Burn averaged 157 mg and Allt dos Mhuicarain fry 144 mg; a further 18 days later fry from the Shelligan Burn averaged 199 mg and Allt dos Mhuicarain fry less than 159 mg. Even after a further ten days i.e. 47 days after stocking, the average weight of fry from Allt dos Mhuicarain had reached only 166 mg.

Except for the fry of the shortest length, the fish from Allt dos Mhuicarain were in poorer condition than those from the Shelligan Burn. The relevant details are given in Table 10.

When planted in Allt dos Mhuicarain the fry had obvious yolk-sacs. Six days after planting, the yolk-sacs were still externally visible on each fry of a sample of ten. Eleven days after planting, 5 of a sample of 25 fry had a slight yellow swelling of the yolk-sac. A sample of ten fry collected the following day had no external yolk-sacs, and, on dissection, no yolk was found internally. No fry collected on later dates contained yolk.

Examination of the gut (stomach and intestine) showed that the fry contained very little food up to at least three weeks after stocking. No food was found in the gut of samples of eight fry collected on each of the first and second days after being planted. One fry out of eight caught on the fifth day after stocking contained one chironomid larva of 1 mm length; the other fry were empty. On the sixth day, six of ten fry contained food and on the seventh day (28th April) five of ten fry contained food. The amount of food present in each gut was very small, the largest amount being three chironomid larvae of 1 mm length. Of 25 fry caught on 2nd

May, 5 fry were empty and 11 contained only one or two food organisms. Of a total of 60 food organisms found in all of the fry (giving a mean of 2.4 per fry) 51 were chironomid larvae of 3 mm or less in length. There was a mean of 1.0 organisms per fry (12 examined) caught on 3rd May and a mean of 2.5 food organisms per fry (13 examined) caught on 11th May.

From about four weeks after stocking the fry caught contained much more food. On 18th May, 18 fry caught all contained food, the fry having a mean of 4.3 organisms (294 μ g dry weight) in their stomachs and a mean of about 4.4 organisms in their intestines. The weight of food in their intestines could not be calculated because of the difficulty of measuring the lengths of many of the fragmented organisms. Five of the fry contained food of terrestrial origin (all adult Diptera) which comprised 19 % of the total food present in the stomachs of all of the fry. On 7th June, ten fry had a mean of 4.6 organisms (598 μ g dry weight, less than 1 % terrestrial) in their stomachs and on 8th June, ten fry had a mean of 4.4 organisms (674 μ g dry weight, less than 1 % terrestrial) in their stomachs.

The bottom fauna of Allt dos Mhuicarain, as well as being quantitatively poor, contained few *Baetis* spp. Less than 3 % of the animals collected in samples from Allt dos Mhuicarain in spring and early summer were *Baetis rhodani* or *B. pumilus* whilst these *Baetis* spp. comprised about 20 % of the bottom fauna from the Shelligan Burn at this time. As *Baetis* species are among the most free-swimming of benthic organisms, occurring frequently in drift fauna on which it seems very probable that fry commence feeding, they are most important fish food organisms. On 9th June *Baetis* spp. accounted for 23 % of the weight of food of fry in the Shelligan Burn, and only 2 % of the weight of food of fry in Allt dos Mhuicarain. *Ephemerella ignita* is another important food of fry in the early stages of feeding. It comprised 13 % of the food of fry in the Shelligan Burn in June but was absent from the food of fry in Allt dos Mhuicarain.

Mills (1964) considered that the heavy mortality of the fry introduced into Allt dos Mhuicarain is a result of the high density of stocking and predation by salmon and trout. However, higher densities of salmon fry occur in the Shelligan Burn and in artificial rearing conditions. Rather it is a lack of correspondence between the stocking density and the stream's capacity to provide the necessary requirements of territory, feeding stations, shelter and food for the normal life of the fry that leads to the high mortality. A heavy mortality could also, of course, result from stocking with unsuitable fry. Under natural conditions, only a small proportion of fry seem to be caught by larger fish. Of 107 salmon and trout of length greater than 55 mm (52 fish greater than 90 mm) caught in the Shelligan Burn in May, June and July, the months when fry are most abundant, only eight contained fry in their stomachs. Of 103 salmon and trout of similar minimum size caught in the same months from the River Almond only six contained fry. Only one fish from both streams contained two fry, the other fish contained one fry only.

Although the mortality of fry in Allt dos Mhuicarain presumably results mainly from exhaustion through lack of food, other biological factors such as increased susceptibility of the fry in poor condition to parasitic and fungoid diseases and capture by predation, and loss in ability to capture prey may be important contributory causes. Ivlev (1961) has shown that the poorer the condition of roach fry after starvation the more intense was their mortality by infection with *Neascus cuticula* (Trematoda) and that the resistance of bream to infection by Saprolegniaceae falls with increasing starvation and poor condition of the fish. In experiments on starving predatory fish Ivlev (l.c.) found that when starvation reaches a certain level the search capacity of tench falls sharply and the fish lose the ability to feed, and die even in the presence of food. With bleak feeding on *Daphnia* spp., Ivlev found that starvation quickly leads to a decrease in the ability of the fry to catch the plankton and that starvation does not produce any intensification of the hunt for food.

DISCUSSION

Little work has been carried out on the factors regulating the capacity of stream environments to support salmon and trout. This capacity will be largely determined by the number of suitable places at which the fish can live and feed. The problems involved, particularly the relationship of the density and size structure of populations of salmon and trout to the physical environment and the distribution and abundance of feeding sites in different environments, are complex, and are the subject of present research. Because of the increasing interest in the growth and population density of salmon and trout in streams, it seems appropriate to discuss together, points which have arisen in the present study and have bearing on these subjects.

If the food supplies available to salmon and trout are to be correctly evaluated, studies of the factors determining the composition of the food eaten by the fish are necessarily of importance. In the present work it has been shown that the type of habitat in which fish are feeding in a stream is a main factor in determining the composition of the food eaten and it has been suggested, with some reason, that the different distributions of the benthic organisms is also probably an important factor. The present writer considers that these factors, rather than the selection by the fish of certain food organisms from among those available, can more reasonably account for a great deal of the variation in the kind and amount of food eaten by fish of similar size. The evidence from the present stomach contents and the tank observations by Kalleberg (1958) suggests that salmon and trout can either feed at times at stations where, presumably, they take drifting organisms brought into their field of view by the current, or alternatively they can comb the substrate for food, when they will find *Hydroptilidae*, *Simulium* spp., *Ancylastrum* spp. and other clinging organisms, as well as the more mobile species which also occur in the drifting fauna. Until it is known which is the more important mode of feeding and until it is known how often any particular species is presented as a possible meal to a salmon or trout, the question of whether or not they select food remains, of course, unanswerable. However, it is unlikely to be as important a factor as Allen (1941a) concluded.

It has been shown that, in the several aspects examined, the Shelligan Burn is richer than the headwaters of the River Almond. The Shelligan Burn, flowing over sandstone and quartzite, contains a higher concentration of inorganic chemical constituents than the River Almond, which flows over quartzite and schist. The surroundings of the Shelligan Burn are agricultural land and cattle pasture with deciduous trees, whereas the surroundings of the River Almond are heather moors and rough sheep-grazing land devoid of deciduous trees. This is reflected in the allochthonic plant material, on which a large proportion of the benthic fauna feeds, being much richer and more varied in the Shelligan Burn than it is in the River Almond. There are also large amounts of submerged mosses in the Shelligan Burn and none in the River Almond. The density of the bottom fauna in the Shelligan Burn is about three times greater, in number and in weight, than that in the River Almond.

Even with this difference in the amounts of bottom fauna, the chief food of salmon and trout, the numerical and biomass densities of 1+ and older fish residing in the River Almond are probably not a great deal less than those in the Shelligan Burn. The salmon and trout in the Shelligan Burn, however, grow at a quicker rate than those in the River Almond and attain, in two years, sizes that are reached only after about three years in the latter stream. It is thus possible that, in these streams at least, it is not so much the density of the salmon and trout populations, as the growth rate of the fish that is regulated by the amount of available food. It is, of course, the production of migratory size fish at an earlier age that chiefly provides the expected greater productivity of fish in the Shelligan Burn when compared with the River Almond.

Salmon and trout living in streams probably cannot see food organisms beyond a short distance, because of obstruction by the substrate and the turbidity of the water. The amount of food the fish receive will depend on the quantities of organisms visible on the substrate at their feeding positions and brought into their field of view by the current. The densities of suitable feeding positions in the Shelligan Burn and River Almond may well be fairly similar. This is possibly due to the similarity between the two streams in the size of their substrate components, their water depth and current flow. There is, however, about three times as much benthic food alone at the feeding positions in the Shelligan Burn as there is at the positions in the River Almond, and this presumably accounts largely for the quicker rate of growth of the salmon and trout in the former stream.

Because of the feeding behaviour described, the considerable variation in growth rate which is found in salmon and trout, is advantageous if the fish are to utilise the range in the quantities of food available in different waters. The capacity for slow development allows salmon and trout to inhabit streams with the sparsest bottom fauna. In such streams, quick growth of fish, even when their population density is low, may not be possible, because of the slow rate at which food is obtained.

As salmon and trout grow faster in the Shelligan Burn than they do in the River Almond, because there is more food in the Shelligan Burn, one would expect that, since trout grow faster than salmon in both streams the trout must occupy the more advantageous feeding positions in the two streams. Trout presumably obtain these by their more aggressive behaviour. Kalleberg (1958) has shown that the components of the threat displays of salmon and trout are very similar and understood by both species. The threat displays of trout are, however, more intense than those of salmon and laboratory observations of aggressive contacts of the two

species 'point to a clear dominance of the trout parr over a salmon parr of about the same size' (Kalleberg l.c.).

A similar stronger aggressive behaviour of trout compared with salmon during their first period of feeding on small organisms might lead to the trout initially obtaining the more favourable feeding stations. Such an early advantage for trout, with its restriction on the growth of salmon, might be expected to lead to the greater variation in the size of 0 + trout and the pronounced difference in growth and size between the salmon and trout as they get older. The alternate spacing of the age classes of salmon and trout in the size-frequency distribution of fish from one area of stream (p. 9) could therefore arise from their early competition for feeding stations.

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SUMMARY

This paper deals with the feeding biology of young salmon and trout in two streams (the Shelligan Burn and the River Almond) of different character in the Central Highlands of Scotland. A study of the feeding of hatchery-reared salmon introduced into a third stream (Allt dos Mhuicairain, Ross-shire) is included.

The Shelligan Burn is richer than the River Almond in the character and vegetation of its surroundings, its ionic concentration, the amount of allochthonic plant material present and the density of its benthic fauna. In both streams the sites studied were chiefly shallow fast-flowing waters but with some pools up to 60 cm depth, and the substrates consisted of stones up to 30 cm lying on smaller stones embedded in gravel and sand.

Salmon and trout in both streams grow most rapidly in May, June and July, less in April, August and September and not at all from October to March. Salmon in the Shelligan Burn reach a mean length of 47 mm in their first year and 96 mm in their second year. The trout in the Shelligan Burn grow faster than the salmon and attain a length of 62 mm in their first year and 130 mm in their second year. The salmon and trout of the River Almond grow at a slower rate than those in the Shelligan Burn, the trout again growing faster than the salmon. Salmon reach a mean length of 43 mm in their first year, 77 mm in their second year and 109 mm in their third year; the respective measurements for trout are 55 mm, 92 mm and 133 mm. There is an alternate spacing of the age classes of salmon and trout in the size frequency distribution of fish in both streams which probably results from the early competition for feeding stations. Salmon of 0 + years are less variable in size than trout of the same age. Where comparison is possible the numerical density and biomass density of the total 1 + and older salmon and trout are not so very dissimilar in the two streams. The expected greater fish productivity of the Shelligan Burn is provided by the earlier production of migratory size fish in this stream.

The variation in the kind and amount of food found in the stomachs of salmon and trout is exceedingly large. A great deal of this variation, and the apparent selection of food by some fish, can probably be attributed to the distribution or behaviour of certain benthic organisms and the type of habitat in which the fish are feeding. Both salmon and trout, caught in pools of the Shelligan Burn, contained significantly more terrestrial organisms and fewer emerging Ephemeroptera than fish caught on the same day from runs of this stream. Salmon from pools in the River Almond contained significantly more emerging Chironomidae and terrestrial organisms than salmon from the runs. Both salmon and trout in pools fed more at the water surface than they did in runs. However, the salmon from the pools contained more of certain benthic organisms and less terrestrial fauna, than trout, differences which must be due to differences in the behaviour or feeding positions of the two species. The paper considers seasonal changes in the amount and kind of food present in the stomachs of salmon and trout and the effect of the changing size-frequency distribution of benthic organisms on the food of the fish. During the spawning period young salmon and trout feed on eggs released by adult salmon and on those disturbed from redds.

The paper includes a discussion of some points bearing on the growth and population density of salmon and trout in the two streams.

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TABLE 1

The chemical analyses of water samples from the Shelligan Burn, River Almond and Allt dos Mhuicairain.
All quantities of ions are in microequivalents per litre.

	pH	SO ₄ ⁼⁼	Cl ⁻	NO ₃ ⁻	HCO ₃ ⁻	NH ₄ ⁺	Na ⁺	K ⁺	Mg ⁺⁺	Ca ⁺⁺
SHELLIGAN BURN										
20 Sept. 1962	7.29	106	133	2	432	7	150	4	132	380
17 Oct. 1962	7.36	108	134	3	460	7	150	4	133	411
15 Nov. 1962	6.99	110	142	9	352	5	142	6	130	330
21 Mar. 1963	6.73	268	157	?	112	?	158	10	99	270
25 Feb. 1964	7.03	171	171	?	196	?	146	8	94	290
RIVER ALMOND										
20 Sept. 1962	7.26	84	104	?	336	?	101	4	120	299
17 Oct. 1962	7.46	91	102	?	356	?	102	6	117	324
21 Mar. 1963	6.79	169	123	?	124	?	110	8	99	199
27 Feb. 1964	7.05	124	140	?	160	?	112	4	115	193
ALLT DOS MHUICARAIN										
7 Nov. 1962	5.73	51	274	?	28	?	232	6	53	60
14 Mar. 1963	5.45	133	217	?	16	?	232	18	51	65
10 Mar. 1964	6.45	77	353	?	48	?	294	16	74	94

? = not calculated

The samples from the Shelligan Burn and River Almond in March 1963 and February 1964 were taken in above normal water conditions after spates which accounts for the lower value for HCO₃⁻, Mg⁺⁺ and Ca⁺⁺ when compared with the previous samples.

TABLE 2

The percentage composition of the bottom fauna in the Shelligan Burn and the River Almond in spring and summer 1962.

	SPRING FAUNA			SUMMER FAUNA	
	Shelligan	Almond		Shelligan	Almond
Leuctra inermis Kempny	14.7	20.1	Naididae	0.6	5.6
Chloroperla torrentium (Pictet)	5.1	1.6			
Amphinemura sulciollis					
(Stephens)	6.3	3.5	Leuctra fusca (L.)	7.4	6.5
Baetis spp.	20.4	31.3	Baetis spp.	8.6	21.4
Rhithrogena semicolorata					
(Curtis)	7.3	4.8	Ephemerella ignita (Poda)	10.6	1.7
Caenis rivulorum Eaton	2.0	4.7	Caenis rivulorum	0.7	15.4
Esolus parallelopipedus					
Müller larvae	4.0	1.0	Esolus parallelopipedus adults	4.4	1.0
			E. parallelopipedus larvae	9.2	2.9
Chironomidae	15.6	13.8	Chironomidae	28.8	18.1
	75.4	80.8		70.3	72.6
Mean number of animals per sample	472	184		261	72

TABLE 3

The mean lengths of salmon and trout colonising an area of the Shelligan Burn after the original population of fish had been removed. Area of stream isolated 59 m².

First electric fishing			Second electric fishing after recolonisation		
9 Oct. 1963			23 Oct. 1963		
	No. measured	Mean length (mm)	No. measured	Mean length (mm)	
Salmon o +	165	44.0	33	42.4	44.0 > 42.4, P = .02—.01
I +	11	96.3	4	93.0	
Trout o +	63	58.5	16	58.6	
I +	15	123.6	3	117.7	

TABLE 4

The variation in the quantity of invertebrate food in samples of fish caught in the Shelligan Burn

Number of food organisms				Dry Weight (μ g) of food		Remarks concerning stomach contents
Fish in sample	Median and range	Fish with more than 2 x median	Fish with more than 2 x median			
			Median and range			
o + Salmon						
June	10	2 — 7 — 14	0	60 — 470 — 1280	2	All benthic organisms One with 11 (520 μ g) emerging and 7 (430 μ g) terrestrial organisms; other fish with benthic fauna only.
Aug.	17	5 — 9 — 30	3	100 — 540 — 1440	1	
Sept.	12	0 — 5 — 25	2	0 — 220 — 1640	5	
I + Salmon						
May	13	1 — 6 — 21	3	20 — 2850 — 5580	0	One with 23 benthic, 1 emerging and 12 terrestrial organisms. Three had 3, 2 and 1 terrestrial organisms among contents.
June	10	0 — 4 — 14	2	0 — 1080 — 4830	3	
Oct.	10	0 — 5 — 36	4	0 — 3530 — 11600	1	
o + Trout						
July	10	2 — 4 — 8	0	60 — 1400 — 3140	2	One with 25 benthic organisms only; one with 7 terrestrial organisms only. One with 38 terrestrial and 2 benthic animals only; one with 7 benthic animals only; one included 4 (16600 μ g) terrestrial animals.
Sept.	14	0 — 3 — 25	3	0 — 470 — 7160	4	
Oct.	15	1 — 7 — 40	3	30 — 1230 — 17880	4	
I + Trout						
June	13	2 — 17 — 47	1	520 — 4300 — 12860	4	One with 41 benthic and 6 terrestrial; one with 6 benthic, 1 emerging and 19 terrestrial; one contained a 21 mm salmonid, 3 benthic and 5 terrestrial organisms.
Oct.	10	0 — 4 — 70	3	0 — 4900 — 79810	3	One with 3 (510 μ g) benthic and 67 (79300 μ g) terrestrial; one with 11 terrestrial only.

TABLE 5

The occasions on which more than seven of the same species of food organism occurred in the stomach contents of salmon and trout from the Shelligan Burn and the River Almond.

Fish with length mm			Date		Numbers of the food organism and other benthic organisms present	Fish with length mm			Date		Numbers of the food organism and other benthic organisms present
S	74	29	5	62	8 Hydroptila + 1	T	92	21	5	62	24 Amphinemura sulcicollis + 10
T	80	29	5	62	8 Hydroptila + 4	S	72	12	6	62	8 1 mm Oreodytes + 4
T	91	29	5	62	8 Hydroptila + 8	S	34	26	6	62	9 1 mm Oreodytes + 3
T	105	12	6	62	53 Hydroptila + 6	T	150	15	3	62	10 Gammarus pulex + 5
S	101	8	5	62	9 Baetis + 23	S	109	21	5	62	319 Simulium + 18
S	105	8	5	62	19 Baetis + 38	S	105	8	5	62	9 Protonemura + 48
S	91	20	8	62	11 Baetis + 57	T	111	26	6	62	9 Agapetus + 13
S	91	19	12	62	56 Baetis + 31 + 7 salmonid eggs	T	94	26	6	62	14 Bibionidae adults (terrestrial) + 12
S	91	19	12	62	12 Baetis + 1	T	74	17	10	62	8 Empididae larvae (terrestrial) + 1
T	80	8	5	62	14 Amphinemura sulcicollis + 15	T	132	17	10	62	66 Empididae larvae (terrestrial) + 4
RIVER ALMOND											
S	52	21	5	62	10 Hydroptila + 8	S	114	21	3	63	10 Baetis, 9 Rhithogena, 27 Leuctra, 9 Isoperla + 10
S	89	29	5	62	26 Hydroptila, 11 Simulium + 45	S	93	29	5	62	9 Simulium + 27
S	100	29	5	62	12 Hydroptila + 36	S	99	12	6	62	13 Simulium + 2
S	105	29	5	62	13 Hydroptila, 12 Simulium + 6	S	108	11	7	62	9 Simulium + 5
S	117	29	5	62	21 Hydroptila + 25	T	114	20	8	62	10 Leuctra + 10
T	71	29	5	62	11 Hydroptila + 3	S	54	21	3	63	52 Leuctra, 11 Amphinemura + 18
T	72	29	5	62	8 Hydroptila + 4	T	84	21	3	63	42 Leuctra + 27
T	114	29	5	62	10 Hydroptila + 4	T	91	21	3	63	9 Leuctra + 11
S	116	12	6	62	20 Hydroptila + 7	T	100	21	3	63	8 Leuctra + 7
S	77	17	10	62	8 Hydroptila + 1	T	120	21	5	62	14 Ceratopogonidae + 7
S	71	26	6	62	8 Baetis + 16	T	71	8	5	62	76 Emerging Chironomidae + 3
S	114	26	6	62	9 Baetis + 16	T	75	8	5	62	85 Emerging Chironomidae + 10
S	79	11	7	62	9 Baetis + 24	T	108	8	5	62	53 Emerging Chironomidae + 5

S = salmon

T = trout

TABLE 6

The stomach contents of salmon and trout caught in pools and runs of the Shelligan Burn and River Almond.
The figures given are the mean numbers of organisms per stomach.

SHELLIGAN BURN 18 Sept. 1963

	Trout 0 +			Trout 1 +			Salmon 0 +			Salmon 1 +	
	Pools	Run 1	Run 2	Pools	Run 1	Run 2	Pools	Run 1	Run 2	Pools	Run 1
No. of fish examined	11	7	6	8	6	10	4	12	5	7	12
Mean size (mm)	54	61	62	122	114	116	43	42	42	97	103
Benthic organisms	17.4	12.7	23.7	14.9	11.3	8.8	5.2	9.7	5.0	24.5	9.2
Chironomidae l.	10.4	5.9	15.7	7.4	1.2	5.3	3.7	6.1	2.6	16.7	4.7
Emerging Baetis spp.	0.0	0.7	0.0	0.1	2.5	3.1	0.0	0.0	0.0	0.0	0.6
Terrestrial fauna	8.8	10.9	12.7	57.6	6.5	11.7	0.7	0.1	0.0	6.5	0.5
Collembola	1.5	0.3	5.8 ²	12.0	0.2	0.3	0.2	0.0	0.0	0.0	0.0
Diptera	2.8	3.4	0.3	15.4	2.3	1.8	0.2	0.0	0.0	2.2	0.1
Hymenoptera	3.7	6.5	5.3	20.6	2.7	6.5	0.2	0.0	0.0	2.0	0.4
Coleoptera	0.5	0.0	0.3	3.7	0.0	0.7	0.0	0.0	0.0	0.2	0.0
Others ¹	0.3	0.7	1.0	5.9	1.3	2.3	0.0	0.1	0.0	2.0	0.0

RIVER ALMOND 21 August 1964

	Trout Shallow pool	Salmon Shallow pool	Salmon Runs
No. of fish examined	10	10	10
Mean size (mm)	102	102	95
Benthic organisms			
Baetis spp.	0.1	0.1	1.1
Hydroptila sp.	8.6	44.2	20.2
Chironomidae l.	0.7	8.8	10.2
Chironomidae p.	4.3	2.5	0.0
Others ¹	1.5	1.5	2.0
Emerging Chironomidae	18.6	14.1	0.0
Terrestrial fauna			
Chironomidae adults	2.1	1.2	0.0
Other Diptera	3.4	2.3	0.1
Hymenoptera	4.1	1.0	0.0
Others ¹	1.5	0.3	0.0

¹ Including adults of Plecoptera, Ephemeroptera and Trichoptera

² 32 in one fish

TABLE 7

The mean number and mean total weight of terrestrial organisms per stomach of salmon and trout from the Shelligan Burn and River Almond. The weights (μ g) are placed in brackets.

		APRIL-MAY	JUNE-JULY	AUGUST-OCT.	NOV.-MARCH
SHELLIGAN BURN					
Salmon	0 +	—	0.8 (70)	0.3 (220)	0.0
	1 + and older	0.0	0.5 (230)	1.7 (510)	0.0
Trout	0 +	—	1.6 (210)	3.2 (1360)	0.4
	1 + and older	1.0 (290)	4.7 (4700)	6.1 (6990)	0.1
RIVER ALMOND					
Salmon	0 +	—	1.0 (20)	2.3 (110)	0.0
	1 + and older	1.6 (690)	3.0 (1490)	0.6 (110)	0.0
Trout	0 +	—	3.0 (112)	3.6 (580)	0.0
	1 + and older	4.7 (1800)	5.8 (750)	24.6 (1490)	0.1

Table 8

The percentage composition by number of the bottom fauna samples and the bottom fauna contents of salmon and trout stomachs from the Shelligan Burn and River Almond.

	FEBRUARY					MAY					JUNE									
	<i>Shelligan</i>		<i>Shelligan</i>			<i>Almond</i>			<i>Shelligan</i>					<i>Almond</i>						
	BF	Ti +	BF	Si +	Ti +	BF	Si +	Ti +	BF	SO +	Si +	TO +	Ti +	BF	Si +	Ti +				
PLECOPTERA .	38	42	31	28	53	22	2	13	13	0	6	0	2	16	2	0				
Leuctra .	22	6	15	10	14	15	1	5	8	0	1	0	1	14	1	0				
Amphinemura	7	16	6	10	28	3	0	5	0	0	0	0	0	0	0	0				
Isoperla .	3	6	2	6	3	0	1	1	0	0	3	0	1	0	0	0				
EPHEMEROPTERA	46	16	29	14	8	45	7	5	23	8	13	3	4	42	15	19				
Bactis . .	33	10	21	7	6	37	5	3	7	0	4	1	1	21	13	15				
TRICHOPTERA .	5	33	5	14	15	5	22	34	6	3	13	0	33	4	22	19				
Hydroptila .	0	0	0	11	10	2	21	33	3	0	6	0	22	0	20	17				
CHIRONOMIDAE .	1	3	16	41	22	15	59	30	37	44	52	77	52	19	49	38				
COLEOPTERA .	0	2	11	1	1	5	0	2	15	39	12	18	3	7	1	19				
Oreodytes .	0	0	0	0	0	0	0	0	0	38	11	14	0	0	1	2				
OTHERS . . .	11	4	7	3	2	9	10	16	5	6	4	3	5	12	10	4				
	JULY				AUGUST				SEPTEMBER											
	<i>Shelligan</i>		<i>Almond</i>		<i>Shelligan</i>		<i>Almond</i>		<i>Shelligan</i>				<i>Almond</i>							
	BF	Si +	BF	Si +	BF	SO +	BF	BF' TO +	BF	SO +	TO +	BF	BF' SO +							
PLECOPTERA .	11	5	8	1	12	2	2	6 0	27	7	2	18	27 2							
Leuctra .	8	1	6	1	7	2	2	5 0	3	2	0	11	16 2							
Amphinemura	0	0	0	0	0	0	0	0 0	12	0	0	1	2 0							
Isoperla .	0	1	0	0	0	0	0	0 0	1	0	0	3	8 0							
EPHEMEROPTERA	11	9	29	16	22	11	5	16 4	23	15	11	15	22 8							
Bactis . .	2	0	23	13	17	10	2	7 2	11	13	7	8	12 6							
TRICHOPTERA .	2	14	1	3	6	2	3	10 3	11	6	20	3	5 1							
Hydroptila .	0	4	0	1	0	1	2	5 3	0	0	0	0	1 1							
CHIRONOMIDAE .	60	59	42	69	35	77	20	61 88	17	65	56	27	41 88							
COLEOPTERA .	8	7	4	0	9	5	1	3 2	9	6	4	1	1 0							
Oreodytes .	0	5	0	0	0	1	0	0 2	0	0	0	0	0 0							
OTHERS . . .	8	6	16	12	16	3	68	5 2	13	2	7	37	5 1							

As salmon and trout from the River Almond are smaller than those of comparable age from the Shelligan Burn, 2 + fish have been grouped with 1 + fish in calculating the figures for the River Almond.

BF = bottom fauna BF' = bottom fauna excluding Naididae S = salmon T = trout

TABLE 9

The size of the food organisms eaten by salmon and trout in the Shelligan Burn. The figures are the percentages of each size in the bottom fauna samples and the stomach contents of fish. The percentage that each size contributes to the weight of the food of 1 + salmon and trout in May and June is given under the column headed 'wt'.

Length mm	MAY			JUNE			JULY			AUGUST			SEPTEMBER					
	BF	SI + wt	TI + wt	BF	SO + wt	TO + wt	SI + wt	TI + wt	TI + wt	BF	SI + wt	BF	SO + wt	TO + wt	BF	SO + wt	TO + wt	
1	2	5	+	2	+	+	10	+	+	+	12	3	7	29	5	17	28	9
2	16	20	1	17	1	1	19	1	22	2	31	21	34	42	41	37	50	42
3	25	20	2	16	3	3	42	7	39	7	29	36	26	21	27	18	6	30
4	15	21	8	29	15	9	12	5	22	13	12	14	14	4	16	9	7	4
5	14	12	10	22	25	5	3	5	7	8	7	9	6	3	5	6	2	9
6	14	7	11	7	13	1	3	4	4	8	5	9	4	1	0	6	7	4
7	6	5	11	3	8	1	0	4	1	3	3	1	5	0	0	4	0	0
8	5	4	19	1	2	1	0	1	4	2	1	4	2	0	3	2	0	2
9	2	4	25	2	14	1	0	0	2	20	+	0	+	0	3	1	0	0
10	1	2	11	1	8	1	0	0	0	1	8	3	1	0	0	1	0	0
> 10	1	0	0	1	11	1	0	0	1	24	2	35	1	0	0	1	0	0

BF = bottom fauna S = salmon T = trout + = present but less than 0.5 %.

TABLE 10

The weights of salmon fry from Allt dos Mhuicarain and the
Shelligan Burn

Length of fry (mm)	Average weights (mg)		Shelligan Burn
	Allt dos Mhuicarain 22 April-3 May	11 May-8 June	
24	114	110	108
25	127	122	134
26	134	138	145
27	144	156	174
28	148	171	200
29	161	177	252

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